



The relationship between female brooding and male nestling provisioning: does climate underlie geographic variation in sex roles?

Jongmin Yoon, Helen R. Sofaer, T. Scott Sillett, Scott A. Morrison and Cameron K. Ghalambor

J. Yoon (*migrate2u@gmail.com*), H. R. Sofaer and C. K. Ghalambor, Dept of Biology, Colorado State Univ., Fort Collins, CO, USA. Present address of JY: Ecological Inst. for Oriental Stork, Korea National Univ. of Education, Cheongju, Republic of Korea. Present address of HRS: U.S. Geological Survey, Fort Collins Science Center, Fort Collins, CO, USA. – T. S. Sillett, Migratory Bird Center, Smithsonian Conservation Biology Inst., National Zoological Park, Washington, DC, USA. – S. A. Morrison, The Nature Conservancy, San Francisco, CA, USA.

Comparative studies of populations occupying different environments can provide insights into the ecological conditions affecting differences in parental strategies, including the relative contributions of males and females. Male and female parental strategies reflect the interplay between ecological conditions, the contributions of the social mate, and the needs of offspring. Climate is expected to underlie geographic variation in incubation and brooding behavior, and can thereby affect both the absolute and relative contributions of each sex to other aspects of parental care such as offspring provisioning. However, geographic variation in brooding behavior has received much less attention than variation in incubation attentiveness or provisioning rates. We compared parental behavior during the nestling period in populations of orange-crowned warblers *Oreothlypis celata* near the northern (64°N) and southern (33°N) boundaries of the breeding range. In Alaska, we found that males were responsible for the majority of food delivery whereas the sexes contributed equally to provisioning in California. Higher male provisioning in Alaska appeared to facilitate a higher proportion of time females spent brooding the nestlings. Surprisingly, differences in brooding between populations could not be explained by variation in ambient temperature, which was similar between populations during the nestling period. While these results represent a single population contrast, they suggest additional hypotheses for the ecological correlates and evolutionary drivers of geographic variation in brooding behavior, and the factors that shape the contributions of each sex.

A central tenet of life-history theory is that investment in current reproduction comes at the expense of future reproduction and survival (Williams 1966, Stearns 1992, Roff 2002). In organisms that provide parental care for their offspring, the optimal level of parental investment should therefore reflect the trade-offs between the fitness benefits and costs associated with parental care over the lifetime of the adults (Trivers 1972, Clutton-Brock 1991, Royle et al. 2012). However, such trade-offs are complicated in organisms that exhibit biparental care because of the inherent conflicts over how much each sex should invest in offspring care versus other activities (Houston et al. 2005). For example, a parent may adjust the amount of care they provide depending on the perceived quality of his or her social mate or the level of investment by their mate (Emlen and Oring 1977, Burley 1988, Westneat and Sargent 1996, Sheldon 2000, Chapman et al. 2003, Magrath and Komdeur 2003). Indeed, most studies assessing the sexual roles have focused on how such conflicts play out by evaluating the changes in parental effort of one sex in response to changes in parental effort of the opposite sex

(reviewed by Harrison et al. 2009). Yet, across populations and species substantial variation also exists in the amount and type of parental care provided by each sex, but the evolutionary, ecological, and social factors responsible for the amount of variation in how much care is provided by each sex still remain unclear (Silver et al. 1985, Møller and Birkhead 1993, Reynolds and Székely 1997, Schwagmeyer et al. 1999, Møller and Cuervo 2000, Cockburn 2006, Olson et al. 2009).

Climatic factors such as ambient temperature or precipitation during the breeding season are thought to influence the amount and form of parental care provided by each sex. However, most latitudinal and altitudinal comparisons have focused on variation in clutch size, despite there being much greater differences in behavioral traits such as nestling provisioning, post-fledging care, or the degree of cooperative breeding (Shaw et al. 2015). Generally, harsh or unpredictable weather conditions coupled with short periods of limited food availability, such as at high altitudes or latitudes, may favor higher overall investment in reproduction to facilitate the survival of offspring (reviewed by

Hille and Cooper 2015). Temperature in particular is often thought to be the most important determinant of male and female behavior during incubation because of the thermal requirements of the eggs and the energetic costs imposed on parents (Martin and Ghalambor 1999, Conway and Martin 2000). However, colder temperatures may also be important during the early nestling period, when young nestlings are ectothermic and dependent on their brooding parent for heat (Lyon and Montgomerie 1985, Lyon et al. 1987, Webb 1993, Badyaev and Ghalambor 2001, Dawson et al. 2005). Later in the nestling period, colder temperatures may result in higher nestling provisioning rates to offset higher thermoregulatory demands of endothermic chicks (Lyon et al. 1987, Hoset et al. 2004). At the same time, low temperature may reduce insect activity and in turn increase foraging time and reduce overall prey delivery to offspring (Avery and Krebs 1984, Low et al. 2008). Collectively, variation in climate along latitudinal or altitudinal gradients could lead to differences in the contributions of each sex between populations, particularly if suboptimal temperatures (i.e. either extremes in cold or heat) force parents to allocate more time to buffering nestlings from environmental temperatures (Johnson and Best 1982, Wiebe and Elchuk 2003, Lobato et al. 2008).

In most passerines, buffering behavior falls on females who are responsible for brooding their nestlings, particularly in the early stages of development when the young are unable to thermoregulate (Dawson and Evans 1960, Olson 1992, Konarzewski 1995). Higher levels of female brooding could in turn require males to compensate by assuming a greater proportion of offspring provisioning (Lyon and Montgomerie 1985, Briskie 1995, Martin and Ghalambor 1999, Badyaev and Ghalambor 2001, Johnson et al. 2007). For example, a global comparative study of songbird populations showed that male help could be indispensable for increasing total nest attentiveness either directly through shared incubation by both sexes or indirectly via male feeding of incubating females (Matysioková and Remeš 2014). However, relatively few comparative studies have specifically investigated how variation in climatic conditions drives differences in patterns of parental care between populations, and the focus of most research has been on the incubation period, rather than on the nestling period when parents must both provision and brood their young (Briskie 1995, Badyaev and Ghalambor 2001, Johnson et al. 2007).

Here, we examine variation in paternal and maternal behavior during the early and late nestling period in two populations of an oscine passerine, the orange-crowned warbler *Oreothlypis celata*. We compare populations at the northern and southern edges of the breeding range, which differ in their life histories and in the ecological conditions they experience. The main goal of this study was to assess patterns of nestling provisioning and brooding behaviors during the nestling stage, and to evaluate how interpopulation variation in parental care was linked with variation in temperature. We predicted that in the high latitude population, lower ambient temperatures would be associated with increased female brooding and a correspondingly higher proportion of male provisioning compared with the population breeding at lower latitude.

Methods

Studied species and areas

The orange-crowned warbler is a small insectivorous passerine with a broad geographic range that spans western and northern North America (Gilbert et al. 2010). We studied the parental behavior of two populations at the northern and southern ends of the breeding distribution. The northern study site was located near Fairbanks, Alaska (64°47'41"N, 147°53'45"W). The Alaska population was studied from 2006 to 2008 and is a long distance migrant that winters along the Gulf Coast of the United States and belongs to the *O. c. celata* subspecies, whose breeding range extends from central Alaska throughout boreal Canada and into the northeastern United States (Gilbert et al. 2010). The southern study site was located on Santa Catalina Island, off the coast of southern California (33°20'56"N, 118°26'59"W). The California population was studied from 2003–2009 and is a resident or short distant migrant to the mainland and belongs to the *O. c. sordida* subspecies, whose breeding distribution is largely confined to the California Channel Islands (Gilbert et al. 2010).

The two populations and habitats that they occupy differ in several important respects. The 88 ha study site for the Alaska population was a spruce *Picea*–birch *Betula*–willow *Salix* dominated habitat, characterized by a short breeding season (50–60 d). In contrast, the 14 ha study site for the California population was an oak *Quercus* and scrub dominated habitat, with a relatively long breeding season (100–120 d). The two populations also exhibited significant life-history differences (Horton et al. 2010, Yoon et al. 2012, 2013, Sofaer et al. 2013). The Alaska population exhibited lower annual adult survival rates (40%) and larger clutch sizes (5–7 eggs), relative to the California population that had a higher annual adult survival (males: 68%, females: 56%; Sofaer et al. 2014) and smaller clutch sizes (2–4 eggs). Breeding density was an order of magnitude lower in Alaska (0.48 territories ha⁻¹ in 2007–2008), compared to California (4.11 territories ha⁻¹ in 2003–2009; Yoon et al. 2012). Both populations were socially monogamous, with female-only incubation for 11–12 d in both populations; males rarely fed their incubating females. After hatching, females brooded altricial nestlings, and both parents contributed to nestling provisioning by delivering insect prey items that consisted largely of lepidopteran larvae (Gilbert et al. 2010). Nestling growth rates were faster in Alaska (Sofaer et al. 2013), and the length of the nestling period was shorter in the Alaska (9.5 d) compared to in California (12.3 d; Sofaer et al. 2013).

We used standardized methods for field data collection at both study sites. Briefly, individual warblers were captured by mist-netting and banded with a unique combination of color bands and a numbered, aluminum U.S. Geological Survey band to identify each individual. At the time of capture, their sex and age were determined based on plumage and morphological traits (Pyle 1997). We found nests and monitored them approximately once every two days to determine their stage and fate. Nests for approximately 30 territorial pairs per site were found and monitored during each breeding season (late February to mid-May in California; mid-May to early July in Alaska).

However, data for only a subset of these monitored pairs are presented here because this study required video data collection. Only those nests that had at least one color-banded parent (for differentiation between the sexes in videos) that survived to the target nestling age, and that had dry weather conditions during that day were used in this study (Table 1). Video recording equipment was also limited, and we prioritized recordings of the late nestling stage over the early nestling stage (see below). Parental behavior data at the nest were collected in Alaska from 2006 to 2008 and in California from 2005 to 2009, except 2007 when birds failed to breed during a severe drought (Langin et al. 2009). Video data were not collected on days with heavy rains; the differences we observed may therefore be conservative because females are expected to brood more in rainy weather, and rainy weather occurred more often in Alaska (the number of precipitation days was 37% of 90 d in Alaska in June of 2006–2008 and 10% of 120 d in California in April of 2005–2009 except 2007).

The contributions of each sex to nestling provisioning

To quantify paternal and maternal provisioning behavior during the nestling stage, we filmed parental activities at the nest using a small bullet camera (Swann, USA) that was remotely connected to a digital camcorder (DCR-TRV900, Sony, Japan) or video recorder (Archos, USA) for the first three hours after sunrise (approximately 03:30–06:30 AKDT in Alaska; approximately 06:30–09:30 PDT in California). Filming occurred 3 d after nestlings hatched (hereafter, the ‘early’ nestling stage) in both populations, and also during the ‘late’ nestling period. The ‘late’ nestling stage videos were collected on the day the primary feathers broke their sheaths, which was also the last day nestlings could be handled without a risk of force fledging; this corresponded to day 6 in Alaska and day 7 in California. Comparisons of early versus late nestling stages allowed for comparisons of how parental roles changed with the increasing energetic demands of the nestlings as they acquired the ability to thermoregulate.

We transcribed nest videos to quantify the following provisioning behaviors for males and females: 1) hourly feeding rate (the number of individual feeding trips h^{-1}) and 2) per-trip food load size, and 3) hourly food delivery rate (the number of individual feeding trips \times food load h^{-1}). Orange-crowned warblers can bring either single or multiple prey items in their beaks while feeding nestlings. Per-trip food load size was estimated as the total area of visible prey items

Table 1. The number of orange-crowned warblers’ nests that were filmed during the early and late nestling stage to investigate sex roles in parental provisioning and brooding behaviors in Alaska and California.

Year	Alaska population		California population	
	Early stage	Late stage	Early stage	Late stage
2005	–	–	–	8
2006	–	9	–	12
2007	2	9	–	–
2008	7	14	8	12
2009	–	–	8	6
Total	9	32	16	38

relative to the parent’s beak size in still frames from nest videos; the mean was calculated for each sex during each video. For example, if the visible area of food was equal to the beak size, the load was scored as 1.0; 0.5 if the load was half the size of the beak; 2.0 if the load was twice the size of the beak. The same criterion was applied for all individuals, and food load scores ranged from 0.5 to 6.5 in our video data.

Female brooding behavior and climatic variation between sites

We quantified the proportion of female brooding time based on the number of minutes spent on the nest during each 3 h video. Brooding time was recorded only when we observed direct contact between the female and nestlings (e.g. time spent perching on the nest rim was excluded). To understand the ecological correlates of variation in female brooding behavior, we tested for differences in temperature and precipitation between populations because colder and wetter conditions should favor increased female brooding of nestlings. We compared ten years of weather data at each site, ending in the last year we had collected behavioral observations (AK: 2008; CA: 2009). For Alaska, we obtained hourly ambient temperature data (i.e. the whole 24-h day) from the Historical Weather Data Archives, NOAA National Severe Storms Laboratory (<<http://data.nssl.noaa.gov>>) and monthly precipitation data from the Alaska Climate Research Center (<<http://climate.gi.alaska.edu>>). For California, temperature and precipitation data were obtained from the Catalina Island Conservancy (<<http://catalinaconservancy.org>>). Weather stations in Alaska and California were located 3.4 and 11.4 km away from our study sites, respectively.

Statistical analyses

We analyzed food load, hourly feeding rate, and food delivery rate in relation to site (Alaska vs California), sex (male vs female) and the two-way interaction (sex \times site) for each nestling stage (early and late), using a linear mixed model with restricted maximum likelihood (REML). Nest ID was included as a random effect to control for observations of males and females recorded from the same nests. We tested for differences in the proportional time that females spent brooding their offspring using a linear mixed model as a function of site, nestling stage, and the two-way interaction (nestling stage \times site); this model included a random effect of nest to account for observations at multiple nestling stages. The proportional time for female brooding in each nestling stage was also re-examined in association with site, ambient temperature during the video recording and the two-way interaction using a general linear model (GLM) without a random effect (because there was one observation per nest in each model). We used a two-sample *t*-test to compare ambient temperature and precipitation in each population for the dates and times during which videos were collected as well as for the month corresponding to the peak of the nestling period (April in CA and June in AK). All statistical analyses were performed in SPSS ver. 16.0 (SPSS, Chicago, IL, USA). We did not need to transform any variables to meet model assumptions. Behavioral measures are presented as means \pm 1 SE.

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.f89h2>> (Yoon et al. 2016).

Results

The contributions of each sex to nestling provisioning

The populations showed striking differences in the division of provisioning effort between the sexes. In California, males and females had similar food load sizes, feeding rates, and

total food delivery rates, but in Alaska, males provided the vast majority of provisioning by each of these three measures (Fig. 1).

Per-trip food loads

We found significant differences in per-trip food loads (i.e. beak-equivalents per trip) between populations and sexes, as well as an interaction between sex and site during both the early (site $F_{1,9.5} = 52.28$, $p < 0.001$; sex $F_{1,9.1} = 26.62$, $p < 0.01$; sex \times site $F_{1,9.1} = 30.45$, $p < 0.001$) and late (site $F_{1,59.2} = 14.71$, $p < 0.001$; sex $F_{1,57.7} = 13.42$, $p = 0.01$; sex \times site $F_{1,57.7} = 21.66$, $p < 0.001$) nestling stages (Fig. 1a, b). During the early nestling stage (Fig. 1a), per-trip food

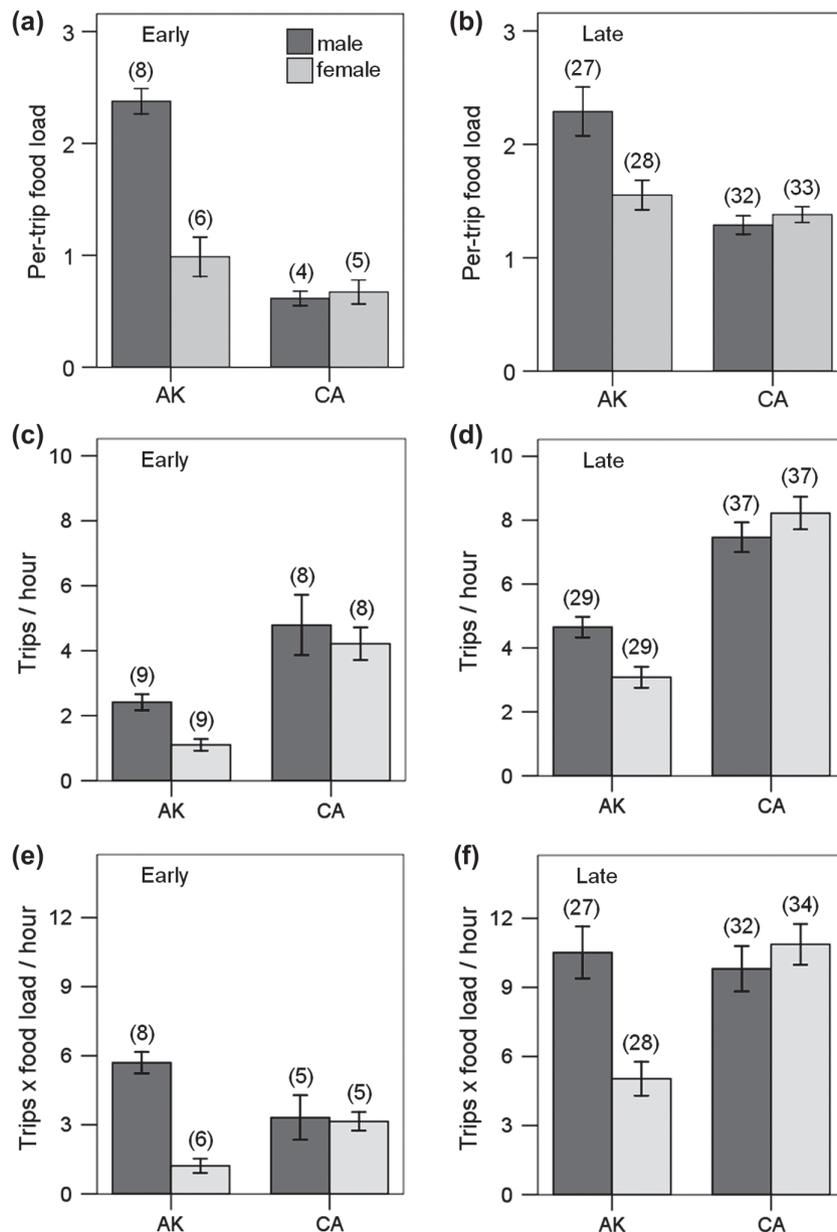


Figure 1. Measures of parental provisioning effort by the sexes of orange-crowned warblers breeding in Fairbanks, Alaska (*Oreothlypis celata*; AK) and on Santa Catalina Island, California (*O. c. sordida*; CA) in the early (day 3 after hatching) and late (day 6 in Alaska; day 7 in California) nestling stages: (a–b) per-trip food loads scored as one if the volume of food load was equal to the beak size (see Methods), (c–d) hourly feeding trips, (e–f) hourly food delivery rate (the number of feeding trips \times food load h^{-1}). Error bars represent means \pm 1 SE (n = numbers of nests).

loads were significantly larger in the population in Alaska than in the population in California; males in Alaska delivered larger food loads per trip than their females, whereas males and females delivered similar-sized food loads in California. Similarly, during the late nestling stage (Fig. 1b), per-trip food loads were significantly larger in the population in Alaska than in the population in California; males in Alaska delivered larger food loads per trip than their females, whereas males and females delivered similar-sized food loads in California.

Hourly feeding trips

The hourly feeding rate (the number of feeding trips h^{-1}) differed between the two populations and marginally differed between the sexes during the early nestling stage (site $F_{1,15} = 22.04$, $p < 0.001$; sex $F_{1,15} = 4.23$, $p = 0.05$; sex \times site $F_{1,15} = 0.68$, $p = 0.42$; Fig. 1c). That is, the higher feeding rate in California was driven by both sexes feeding more frequently than their counterparts in Alaska; the marginally significant difference between the sexes was largely driven by Alaska females feeding young at a lower rate than their males although a two-way interaction was not significant. The same general patterns were observed during the late nestling stage (Fig. 1d). California parents provisioned late-stage nestlings at a higher feeding rate than did Alaska parents, without a significant difference between the sexes, but there was a significant two-way interaction driven by a difference in male and female feeding rate in Alaska (mixed model: site $F_{1,128} = 81.40$, $p < 0.001$; sex $F_{1,128} = 0.86$, $p = 0.36$; sex \times site $F_{1,128} = 6.99$, $p = 0.01$; Fig. 1d). In Alaska, females made fewer feeding trips per hour to the nest than did males during the late nestling stage, whereas the sexes did not differ in their feeding rate in California.

Hourly food delivery rate

When food load was incorporated into hourly food delivery rate (the number of feeding trips \times food load h^{-1}), the contribution of males in Alaska to nestling provisioning was further enhanced (Fig. 1e, f). Each hour, males delivered more food to the nest than did their females in

Alaska whereas this food delivery rate did not differ between sexes in California. This was true during both the early (Fig. 1e; site $F_{1,20} = 0.16$, $p = 0.69$; sex $F_{1,20} = 16.97$, $p < 0.01$; sex \times site $F_{1,20} = 14.58$, $p < 0.01$) and late (Fig. 1f; site $F_{1,58.1} = 5.60$, $p = 0.02$; sex $F_{1,57.1} = 8.65$, $p < 0.01$; sex \times site $F_{1,57.1} = 17.46$, $p < 0.001$) nestling stages. The overall food delivery rate did not differ between the two populations during the early nestling stage, but was higher in California during the late nestling stage. At both stages, females delivered significantly less food than either Alaska males or either sex in California, resulting in significant differences between the sexes and the two-way interaction.

Female brooding behavior and climatic variation between sites

Female brooding behavior

The proportion of time females spent brooding was significantly higher in Alaska than in California, and it significantly decreased from the early to late nestling stage in both populations, with no significant interaction between stage and population (site $F_{1,71.9} = 38.53$, $p < 0.001$; stage $F_{1,12.3} = 126.00$, $p < 0.001$; stage \times site $F_{1,12.3} = 1.40$, $p = 0.26$; Fig. 2a). That is, the magnitude of the decline from the early to late nestling stage was similar between populations. There was no relationship between ambient temperature and brooding behavior. During the early nestling stage, when sample sizes were smaller, the proportion of time females spent brooding was not explained by site, ambient temperature, or the two-way interaction (site $F_{1,12} = 1.77$, $p = 0.21$; temperature $F_{1,12} = 0.15$, $p = 0.71$; site \times temperature $F_{1,12} = 0.09$, $p = 0.77$). During the late nestling stage, variation in female brooding behavior was explained only by site (site $F_{1,57} = 8.66$, $p < 0.01$; temperature $F_{1,57} = 3.27$, $p = 0.08$; site \times temperature $F_{1,57} = 2.74$, $p = 0.10$). Furthermore, the ambient temperature during videos did not significantly differ between the Alaska and California sites during the early (t test: $t_{7.8} = -0.62$, $p = 0.56$) or late ($t_{58} = -0.13$, $p = 0.90$) nestling stages.

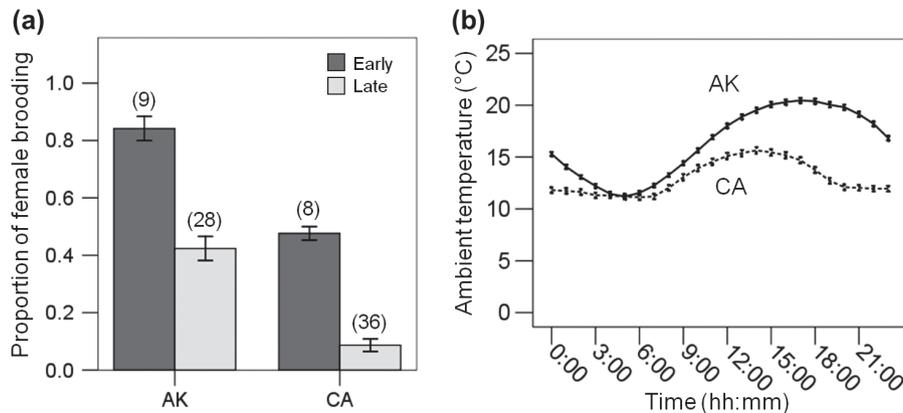


Figure 2. Nestling brooding behavior of female orange-crowned warblers and climate variation between Fairbanks, Alaska (AK) and Santa Catalina Island, California (CA): (a) proportional female brooding time (brooding min/videotaped min) in the early (day 3 after hatching) and late (day 6 in Alaska; day 7 in California) nestling stages from the 3 h nest videos in Alaska and California and (b) hourly means of ambient temperature ($^{\circ}\text{C}$) for 10 yr in Fairbanks, Alaska (June in 1999–2008) and Santa Catalina Island, California (April in 2000–2009). Error bars represent means \pm 1 SE.

Climatic variables

Ambient temperatures during the nestling period (June in 1999–2008 for Alaska and April in 2000–2009 for California; Fig. 2b) were on average higher in Alaska ($16.36 \pm 0.18^\circ\text{C}$, $n = 294$) than in California ($12.94 \pm 0.26^\circ\text{C}$, $n = 255$). These results are consistent with the interior continental climate of Fairbanks and the moderate marine climate of Santa Catalina Island. In the comparison of ten-year ambient temperatures between two study areas, the average of daily mean temperature was approximately 3.43°C higher in Alaska than in California ($t_{462} = 10.81$, $p < 0.001$), the average of daily minimum temperatures was approximately 0.80°C higher in Alaska (t test: $t_{547} = 2.95$, $p < 0.01$), and the average of daily maximum temperatures was also approximately 4.94°C higher in Alaska ($t_{472} = 12.77$, $p < 0.001$). Precipitation during the month containing the peak of the nestling period was significantly higher in Alaska (27.45 ± 5.11 mm) than in California (0.95 ± 0.48 mm; t test: $t_{19} = 5.17$, $p = 0.01$).

Discussion

Our study documented clear differences in the parental contributions of male and female *O. celata* breeding in central Alaska and southern California, but these differences were not explained by temperature. In California, males and females provisioned their nestlings at similar rates and brought similar sized food loads. In contrast, males in Alaska both fed more frequently and brought more food per feeding trip, resulting in substantially higher food delivery by males than by females. This pattern of high provisioning by males in Alaska appeared to compensate for and facilitate the high brooding rates by females, who spent approximately 80 and 50% of the early and late nestling stages brooding their offspring, respectively. This result is in line with other studies documenting the positive relationship between males' direct or indirect help (i.e. shared incubation or incubation feeding) and total nest attentiveness during incubation (Lyon and Montgomerie 1985, Badyaev and Ghalambor 2001, Matysioková and Remeš 2014). In previous studies, cold, unpredictable, and extreme environments have been invoked as explanations for altitudinal and latitudinal variation in patterns of avian parental care (Briskie 1995, Badyaev and Ghalambor 2001, Summers and Nicoll 2004, Johnson et al. 2007, Matysioková and Remeš 2010, 2014). However, the expectation that colder temperatures account for the higher rates of brooding in Alaska compared with California was not supported. Indeed, temperatures were warmer during the nestling period in Alaska compared to California (Fig. 2b), and did not differ between sites during video recordings. This result challenges the assumption that ambient temperature is the primary ecological driver of geographic variation in brooding behavior and suggests that studies of parental contributions should consider other ecological drivers and the consequences time spent brooding has on male and female provisioning.

Understanding male and female contributions to parental care is a major area of research because both social and ecological contexts affect the relationship between parental expenditure and parental and offspring physiological

condition and fitness. Conflict between the sexes arises because each parent benefits from a high total investment in offspring, while simultaneously trying to minimize their personal expenditure (Houston et al. 2005). Within populations, studies manipulating the contributions of one sex have tested the ability and willingness of the other sex to compensate (Wright and Cuthill 1989). In addition, many studies have asked how male contributions can be shaped by the opportunities for extra-pair copulations and by confidence in paternity, and have often explored how hormonal variation may underlie observed behavioral variation (reviewed by Ketterson and Nolan 1994, Schwagmeyer et al. 1999, Møller and Cuervo 2000). The conflict between the sexes becomes even more nuanced when multiple dimensions of parental care are considered and sex-specific contributions differ among these dimensions. For example, in socially monogamous passerines, females may do most of the incubation while males provide more territorial defense (Clutton-Brock 1991). In species where biparental care is maintained but males do more incubation and brooding, there may be a general reversal of sex roles, such that the male also provides more feeding (Rossmann et al. 2009). Our Alaska study population provides an example where one sex provides most of the feeding while the other is solely responsible for brooding; the contrast with California supports work showing how the relative contributions to feeding depend on the ecological context (Wittenberger 1982). Although studies have investigated male and female contributions to feeding in species in which only the female broods (Conrad and Robertson 1993) and in species in which both sexes brood (Carere and Alleva 1998), these studies have not been synthesized to evaluate whether there are general patterns in how the sexes divide their time and energy to different components of parental care.

The different types of care that parents provide make it difficult to summarize the relative contributions of each sex because the energetic expenditure associated with each type of care is difficult to determine. In particular, the costs of brooding young are poorly understood, making it challenging to compare contributions to brooding and feeding. Some work has suggested brooding young may create a sufficient energetic and time constraint to cause declines in female condition (Chastel and Kersten 2002), while other studies have found no evidence for such costs (Sanz and Moreno 1995). The relative costs of brooding and feeding affect patterns of energetic expenditure with nestling age and brood size, because brooding declines with these factors (Clark 1985), while feeding rates increase. In our California study population, feeding rates of females and males were approximately equal both early and late in the nestling period, but females also brooded young nestlings. This suggests that females' relative contribution was higher early in the nestling period. It is more difficult to summarize the relative contributions and costs of care in Alaska, when females brooded much of the time but males provided more food. These costs will also vary with factors that affect the costs of brooding (e.g. nestling age, brood size, and temperature), as well as with food availability and the costs of provisioning.

The most striking results of our study are the high brooding rates in Alaska compared with California despite no differences in ambient temperature (Fig. 2). Previous studies

within populations have shown that low temperatures generally forced females to brood their young, and high precipitation caused parental feeding rates to decrease, resulting in reduction in the growth and survival of the nestlings (Murphy 1983, Rosa and Murphy 1994). However, our results suggest that between our two study populations, weather conditions may not be the primary factor underlying differences in these parental traits. We recognize the limitations of our study, as it represents only a single correlative contrast, and a diversity of unmeasured environmental differences exist between birds in California and Alaska. We also cannot rule out that the described behavioral patterns might reflect an evolutionary response to climate in the past (Wesolowski 1994, Ball and Ketterson 2008), rather than current climatic conditions. Nevertheless, even in the absence of obvious ecological drivers of divergence, our results, do call into question commonly held assumptions regarding the relationships among temperature, brooding behavior, and sex-specific provisioning rates.

The suite of environmental differences between our study populations points to potential areas for future research and additional hypotheses that could be tested. For example, high food availability and long days may facilitate high rates of brooding by allowing most of the provisioning to be done by the male, and long days may also relax time constraints on females. Wolf et al. (1990) found that experimental removal of males resulted in females having to spend less time brooding, and more time provisioning their offspring (see also Sasvári 1986, Johnson et al. 1992, Johnson and Kermott 1993, Bjørnstad and Lifeld 1996). However, these factors potentially explain why observed brooding patterns in Alaska may be possible, but not why they are favored. One possibility is that brooding enables faster growth, as nestlings in Alaska grow more quickly (Sofaer et al. 2013), and rapid growth may be favored by the short breeding season. Energy provided to nestlings in the form of food must be allocated to the competing demands of growth, development, thermoregulation, and begging behavior (Ricklefs 1974, Dunn 1980, Olson 1992, Pearson 1998, Węgrzyn 2013). Any parental behaviors that reduce thermoregulatory costs (e.g. constructing a more insulated nest: Rohwer and Law 2010; a warmer nest site: Dawson et al. 2005, Pérez et al. 2008; increased female brooding: Rensel et al. 2010) could help speed up growth and maturation. In addition, because brooding elevates the body temperature and metabolism of the offspring, the physiological processes associated with the ability to digest food and allocate nutrients to rapidly growing tissues could be enabled by higher brooding rates (Johnson and Kermott 1993). Previous studies have suggested a trade-off between growth and endothermy (Dawson and Evans 1960, Węgrzyn 2013), and we speculate that brooding may play an important role in mediating this trade-off.

In conclusion, the ecological factors that alter how sexes allocate time and energy to different components of parental care and the consequences of this variation remain largely unresolved. Whether geographic variation in female brooding behavior consistently leads to changes in the sex-specific contributions to nestling feeding will require more comparative studies of populations occupying diverse environments. It may be that the factors that influence rates of brooding within populations differ from those that explain

variation between populations. For example, within populations, parents often spend less time brooding larger broods because of their greater capacity for homeothermy (Clark 1985), but we documented the opposite pattern between populations. Like incubation attentiveness, brooding behavior may vary along the life history continuum and may be associated with high parental investment more generally. Growth rates also vary along the life history continuum, so comparative studies of brooding, growth, and male and female feeding rates may provide a better understanding of both the correlates and drivers of variation in parental contributions.

Acknowledgements – This study was funded by The Nature Conservancy, the Smithsonian Inst., and Colorado State Univ. The Catalina Island Conservancy (CIC) generously provided affordable housing and vehicles. Frank Starkey and Carlos de la Rosa of the CIC provided logistical support, and many people helped with the fieldwork, especially Luke Caldwell, Brent Horton, Kathryn Langin, and Hannah Montag. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The present study involved marking individual warblers, mapping their territory boundaries, and video recording of breeding males and females at the nest. All research was conducted under ASAB/ABS guidelines and approved by the Institutional Animal Care and Use Committees of Colorado State Univ. (08-342A-01) and the Smithsonian's National Zoological Park (04-26, 07-24).

References

- Avery, M. I. and Krebs, J. R. 1984. Temperature and foraging success of great tits *Parus major* hunting for spiders. – *Ibis* 126: 33–38.
- Badyaev, A. V. and Ghalambor, C. K. 2001. Evolution of life histories along elevational gradients: trade-off between parental care and fecundity. – *Ecology* 82: 2948–2960.
- Ball, G. F. and Ketterson, E. D. 2008. Sex differences in the response to environmental cues regulating seasonal reproduction in birds. – *Phil. Trans. R. Soc. B* 363: 231–246.
- Bjørnstad, G. and Lifeld, J. T. 1996. Male parental care promotes early fledging in an open-nester, the willow warbler *Phylloscopus trochilus*. – *Ibis* 138: 229–235.
- Briskie, J. V. 1995. Nesting biology of the yellow warbler at the northern limit of its range. – *J. Field Ornithol.* 66: 531–543.
- Burley, N. 1988. The differential-allocation hypothesis: an experimental test. – *Am. Nat.* 132: 611–628.
- Carere, C. and Alleva, E. 1998. Sex differences in parental care in the common swift (*Apus apus*): effect of brood size and nestling age. – *Can. J. Zool.* 76: 1382–1387.
- Chapman, T., Arnqvist, G., Bangham, J. and Rowe, L. 2003. Sexual conflict. – *Trends Ecol. Evol.* 18: 41–47.
- Chastel, O. and Kersten, M. 2002. Brood size and body condition in the house sparrow *Passer domesticus*: the influence of brooding behaviour. – *Ibis* 144: 284–292.
- Clark, L. 1985. Consequences of homeothermic capacity of nestlings on parental care in the European starling. – *Oecologia* 65: 387–393.
- Clutton-Brock, T. H. 1991. The evolution of parental care. – Princeton Univ. Press.
- Cockburn, A. 2006. Prevalence of different models of parental care in birds. – *Proc. R. Soc. B* 273: 1375–1383.
- Conrad, K. F. and Robertson, R. J. 1993. Patterns of parental provisioning by eastern phoebes. – *Condor* 95: 57–62.

- Conway, C. J. and Martin, T. E. 2000. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. – *Evolution* 54: 670–685.
- Dawson, W. R. and Evans, F. C. 1960. Relation of growth and development to temperature regulation in nestling vesper sparrows. – *Condor* 62: 329–340.
- Dawson, R. D., Lawrie, C. C. and O'Brien, E. L. 2005. The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. – *Oecologia* 144: 499–507.
- Dunn, E. H. 1980. On the variability in energy allocation of nestling birds. – *Auk* 97: 19–27.
- Emlen, S. T. and Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. – *Science* 197: 215–223.
- Gilbert, W. M., Sogge, M. K. and Van Riper III, C. 2010. Orange-crowned warbler (*Oreothlypis celata*). – In: Poole, A. (ed.), *The birds of North America online*. Cornell Lab of Ornithology, Ithaca, <<http://bna.birds.cornell.edu/bna/species/101>>.
- Harrison, F., Barta, Z., Cuthill, I. and Székely, T. 2009. How is sexual conflict over parental care resolved? A meta-analysis. – *J. Evol. Biol.* 22: 1800–1812.
- Hille, S. M. and Cooper, C. B. 2015. Elevational trends in life histories: revising the pace-of-life framework. – *Biol. Rev.* 90: 204–213.
- Horton, B. M., Yoon, J., Ghalambor, C. K., Moore, I. T. and Sillert, T. S. 2010. Seasonal and population variation in male testosterone levels in breeding orange-crowned warblers (*Vermivora celata*). – *Gen. Comp. Endocrinol.* 168: 333–339.
- Hoset, K. S., Espmark, Y., Moksnes, A., Haugan, T., Ingebrigtsen, M. and Lier, M. 2004. Effect of ambient temperature on food provisioning and reproductive success in snow buntings *Plectrophenax nivalis* in the high arctic. – *Ardea* 92: 239–246.
- Houston, A. I., Székely, T. and McNamara, J. M. 2005. Conflict between parents over care. – *Trends Ecol. Evol.* 20: 33–38.
- Johnson, E. J. and Best, L. B. 1982. Factors affecting feeding and brooding of gray catbird nestlings. – *Auk* 99: 148–156.
- Johnson, L. S. and Kermott, L. H. 1993. Why is reduced male parental assistance detrimental to the reproductive success of secondary female house wrens? – *Anim. Behav.* 46: 1111–1120.
- Johnson, L. S., Merkle, M. S. and Kermott, L. H. 1992. Experimental evidence for importance of male parental care in monogamous house wrens. – *Auk* 109: 662–664.
- Johnson, L. S., Brubaker, J. L., Ostlind, E. and Balenger, S. L. 2007. Effect of altitude on male parental expenditure in mountain bluebirds (*Sialia currucoides*): are higher-altitude males more attentive fathers? – *J. Ornithol.* 148: 9–16.
- Ketterson, E. D. and Nolan Jr, V. 1994. Male parental behavior in birds. – *Annu. Rev. Ecol. Syst.* 25: 601–628.
- Konarzewski, M. 1995. Allocation of energy to growth and respiration in avian postembryonic development. – *Ecology* 76: 8–19.
- Langin, K. M., Sillert, T. S., Yoon, J., Sofaer, H. R., Morrison, S. A. and Ghalambor, C. K. 2009. Reproductive consequences of an extreme drought for orange-crowned warblers on Santa Catalina and Santa Cruz Islands. – In: Damiani, C. C. and Garcelon, D. K. (eds), *Proceedings of the Seventh California Islands Symposium*, Arcata, CA. Inst. for Wildlife Studies, pp. 293–300.
- Lobato, E., Merino, S., Moreno, J., Morales, J., Tomás, G., Martínez-de la Puente, J., Osorno, J. L., Kuchar, A. and Möstl, E. 2008. Corticosterone metabolites in blue tit and pied flycatcher droppings: effects of brood size, ectoparasites and temperature. – *Horm. Behav.* 53: 295–305.
- Low, M., Eggers, S., Arlt, D. and Pärt, T. 2008. Daily patterns of nest visits are correlated with ambient temperature in the northern wheatear. – *J. Ornithol.* 149: 515–519.
- Lyon, B. E. and Montgomerie, R. D. 1985. Incubation feeding in snow buntings: female manipulation or indirect male parental care? – *Behav. Ecol. Sociobiol.* 17: 279–284.
- Lyon, B. E., Montgomerie, R. D. and Hamilton, L. D. 1987. Male parental care and monogamy in snow buntings. – *Behav. Ecol. Sociobiol.* 20: 377–382.
- Magrath, M. J. L. and Komdeur, J. 2003. Is male care compromised by additional mating opportunities? – *Trends Ecol. Evol.* 18: 424–430.
- Martin, T. E. and Ghalambor, C. K. 1999. Males feeding females during incubation. I. Required by microclimate or constrained by nest predation? – *Am. Nat.* 153: 131–139.
- Matysioková, B. and Remeš, V. 2010. Incubation feeding and nest attentiveness in a socially monogamous songbird: role of feather colouration, territory quality and ambient environment. – *Ethology* 116: 596–607.
- Matysioková, B. and Remeš, V. 2014. The importance of having a partner: male help releases females from time limitation during incubation in birds. – *Front. Zool.* 11: 24.
- Møller, A. P. and Birkhead, T. R. 1993. Certainty of paternity covaries with paternal care in birds. – *Behav. Ecol. Sociobiol.* 33: 261–268.
- Møller, A. P. and Cuervo, J. J. 2000. The evolution of paternity and paternal care in birds. – *Behav. Ecol.* 11: 472–485.
- Murphy, M. T. 1983. Clutch size in the eastern kingbird: factors affecting nestling survival. – *Auk* 100: 326–334.
- Olson, J. M. 1992. Growth, the development of endothermy, and the allocation of energy in red-winged blackbirds (*Agelaius phoeniceus*) during the nestling period. – *Physiol. Zool.* 65: 124–152.
- Olson, V. A., Webb, T. J., Freckleton, R. P. and Székely, T. 2009. Are parental care trade-offs in shorebirds driven by parental investment or sexual selection? – *J. Evol. Biol.* 22: 672–682.
- Pearson, J. T. 1998. Development of thermoregulation and posthatching growth in the altricial cockatiel *Nymphicus hollandicus*. – *Physiol. Zool.* 71: 237–244.
- Pérez, J. H., Ardia, D. R., Chad, E. K. and Clotfelter, E. D. 2008. Experimental heating reveals nest temperature affects nestling condition in tree swallows (*Tachycineta bicolor*). – *Biol. Lett.* 4: 468–471.
- Pyle, P. 1997. Identification guide to North American birds – part 1. – Slate Creek Press.
- Rensel, M. A., Wilcoxon, T. E. and Schoech, S. J. 2010. The influence of nest attendance and provisioning on nestling stress physiology in the Florida scrub-jay. – *Horm. Behav.* 57: 162–168.
- Reynolds, J. D. and Székely, T. 1997. The evolution of parental care in shorebirds: life histories, ecology, and sexual selection. – *Behav. Ecol.* 8: 126–134.
- Ricklefs, R. E. 1974. Energetics of reproduction in birds. – In: Paynter, R. A. (ed.), *Avian energetics*. Nuttall Ornithological Club, pp. 152–292.
- Roff, D. A. 2002. The evolution of life histories. – Chapman and Hall.
- Rohwer, V. G. and Law, J. S. Y. 2010. Geographic variation in nests of yellow warblers breeding in Churchill, Manitoba, and Elgin, Ontario. – *Condor* 112: 596–604.
- Rosa, S. M. and Murphy, M. T. 1994. Trade-offs and constraints on eastern kingbird parental care. – *Wilson Bull.* 106: 668–678.
- Rossmann, E., Blaum, N., Höntschi, K. and Jeltsch, F. 2009. Sex-related parental care strategies in the lesser spotted woodpecker *Picoides minor*: of flexible mothers and dependable fathers. – *J. Avian Biol.* 40: 28–33.
- Royle, N. J., Smiseth, P. T. and Kölliker, M. 2012. The evolution of parental care. – Oxford Univ. Press.
- Sanz, J. J. and Moreno, J. 1995. Mass loss in brooding female pied flycatchers *Ficedula hypoleuca*: no evidence for reproductive stress. – *J. Avian Biol.* 26: 313–320.

- Sasvári, L. 1986. Reproductive effort of widowed birds. – *J. Anim. Ecol.* 55: 553–564.
- Schwagmeyer, P. L., St Clair, R. C., Moodie, J. D., Lamey, T. C., Schnell, G. D. and Moodie, M. N. 1999. Species differences in male parental care in birds: a reexamination of correlates with paternity. – *Auk* 116: 487–503.
- Shaw, P., Owoyesigire, N., Ngabirano, S. and Ebbutt, D. 2015. Life history traits associated with low annual fecundity in a central African parid: the stripe-breasted tit *Parus fasciiventer*. – *J. Ornithol.* 156: 209–221.
- Sheldon, B. C. 2000. Differential allocation: tests, mechanisms and implications. – *Trends Ecol. Evol.* 15: 397–402.
- Silver, R., Andrews, H. and Ball, G. F. 1985. Parental care in an ecological perspective: a quantitative analysis of avian subfamilies. – *Am. Zool.* 25: 823–840.
- Sofaer, H. R., Chapman, P. L., Sillett, T. S. and Ghalambor, C. K. 2013. Advantages of nonlinear mixed models for fitting avian growth curves. – *J. Avian Biol.* 44: 469–478.
- Sofaer, H. R., Sillett, T. S., Langin, K. M., Morrison, S. A. and Ghalambor, C. K. 2014. Partitioning the sources of demographic variation reveals density-dependent nest predation in an island bird population. – *Ecol. Evol.* 4: 2738–2748.
- Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press.
- Summers, R. W. and Nicoll, M. 2004. Geographical variation in the breeding biology of the purple sandpiper *Calidris maritima*. – *Ibis* 146: 303–313.
- Trivers, R. L. 1972. Parental investment and sexual selection. – In: Campbell, B. (ed.), *Sexual selection and the descent of Man*. Aldine, pp. 136–179.
- Webb, D. R. 1993. Maternal-nestling contact geometry and heat transfer in an altricial bird. – *J. Therm. Biol.* 18: 117–124.
- Węgrzyn, E. 2013. Resource allocation between growth and endothermy allows rapid nestling development at low feeding rates in a species under high nest predation. – *J. Avian Biol.* 44: 383–389.
- Wesolowski, T. 1994. On the origin of parental care and the early evolution of male and female parental roles in birds. – *Am. Nat.* 143: 39–58.
- Westneat, D. F. and Sargent, R. C. 1996. Sex and parenting: the effects of sexual conflict and parentage on parental strategies. – *Trends Ecol. Evol.* 11: 87–91.
- Wiebe, K. L. and Elchuk, C. L. 2003. Correlates of parental care in northern flickers *Colaptes auratus*: do the sexes contribute equally while provisioning young? – *Ardea* 91: 91–101.
- Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. – *Am. Nat.* 100: 687–690.
- Wittenberger, J. F. 1982. Factors affecting how male and female bobolinks apportion parental investments. – *Condor* 84: 22–39.
- Wolf, L., Ketterson, E. D. and Nolan Jr, V. 1990. Behavioural response of female dark-eyed juncos to the experimental removal of their mates: implications for the evolution of male parental care. – *Anim. Behav.* 39: 125–134.
- Wright, J. and Cuthill, I. 1989. Manipulation of sex differences in parental care. – *Behav. Ecol. Sociobiol.* 25: 171–181.
- Yoon, J., Sillett, T. S., Morrison, S. A. and Ghalambor, C. K. 2012. Breeding density, not life history, predicts interpopulation differences in territorial aggression in a passerine bird. – *Anim. Behav.* 84: 515–521.
- Yoon, J., Sillett, T. S., Morrison, S. A. and Ghalambor, C. K. 2013. Male's return rate, rather than territory fidelity and breeding dispersal, explains geographic variation in song sharing in two populations of an oscine passerine (*Oreothlypis celata*). – *Behav. Ecol. Sociobiol.* 67: 1691–1697.
- Yoon, J., Sofaer, H. R., Sillett, T. S., Morrison, S. A. and Ghalambor, C. K. 2016. Data from: The relationship between female brooding and male nestling provisioning: does climate underlie geographic variation in sex roles? – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.f89h2>>.